

# **Seagrass-associated macrobenthic functional diversity and functional structure along an estuarine gradient**

Running head: Estuarine macrobenthic functional diversity

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**Abstract**

Changes in the relative importance of the 27 component functional groups (FGs) of seagrass-associated macrobenthos were assessed up the long axis of an estuarine system. Although previously observed division of the estuary into two sections with respect to species diversity was confirmed, this did not correspond to any functional compartmentalisation.

Functionally, division was into the terminal extremes and the large intervening marine/lagoonal/lower-estuarine zone, within which no linear segregation of sites occurred. 40% of individual FGs in the latter showed no variation at all, and variation in the remainder was only axially related in two cases, one positive and one negative. Overall structure of the dominant FGs at each locality remained uniform, although rank orders of proportional importance varied widely. Only one major marine/lagoonal FG failed to penetrate the upper estuary at the time of sampling. Estuarine components may change spatially, sometimes dramatically, but overall functional pattern shows considerably less change than the species numbers usually used in characterisation.

Key words: Biodiversity - Biological traits – Estuarine gradients -  
Functional diversity – Knysna - Macrobenthos - Seagrass

## 1. Introduction

Following the classic early work of Remane (1934), organisms in transitional brackish waters have largely been viewed as a suite of coastal marine species capable of penetrating waters of lower salinity to differing degrees, each dependent on its tolerance limit to dilution of — or to fluctuations in — their external milieu (Barnes, 1989; Montague and Ley, 1993; Josefson and Hansen, 2004). Together such organisms usually create a pattern of initially gradual but accelerating decline in species richness/density with increasing distance upstream, as more and more species reach their limit and are not replaced (Cognetti and Maltagliati, 2000; Attrill and Rundle, 2002; Whitfield *et al.*, 2012). Although this Baltic Sea based 'Remane paradigm' (Remane, 1934; 1971) has become the established model for estuarine diversity patterns (Attrill, 2002; Whitfield *et al.*, 2012), it is clearly not without problems when applied to fluctuating estuaries rather than to the relatively constant inland brackish seas of its inception (Attrill, 2002; De Biasi *et al.*, 2003; Teske and Wooldridge, 2004; Whitfield *et al.*, 2012; Blanchet *et al.*, 2014). One factor modifying its application to benthic species has been shown to be the occurrence of a covering of seagrass over the sediment. Along a <5-35 salinity gradient in the Knysna estuarine system in warm-temperate South Africa, i.e. that segment of the estuary along which the dwarf-eelgrass *Zosterella capensis* occurs, Barnes and Ellwood (2012) found zones of considerable stability in the associated macrobenthic faunal biodiversity separated by relatively sharp discontinuities.

The data underpinning this Remane paradigm are the presence or absence of individual species at points along the gradient. However, ecologists routinely also group organisms by functional considerations such as the nature of their niches and hence an available ecological alternative is to consider functional structure and diversity rather than taxonomic identity and composition (see, e.g., Tilman et al., 1997; Bremner et al., 2003; Cadotte et al., 2011; Magalhães and Barros, 2011). Indeed, there is a practical advantage in this approach in that conservation of species biodiversity will not in itself maintain ecosystem health or function. Diaz and Cabido (2001) argue that as the contribution of individual species to the system as a whole varies so markedly, conservation efforts should instead focus on functional traits and functional diversity. Nevertheless, in spite of the advantages of a functional approach (Tilman et al., 1997) and the fact that it has been available for decades (McGill et al., 2006), the large majority of studies into ecosystem structure continue to use species as their basic unit (Feld et al., 2009; van der Linden et al., 2012).

The general functional ecology of seagrass faunas has received considerable attention (e.g. Duffy et al., 2001; Boström et al., 2006; Plummer et al., 2012; Yamada et al., 2014), including within various estuarine systems (e.g. Yamada et al., 2007; Magalhães and Barros, 2011; van der Linden et al., 2012; Dolbeth et al., 2013). Species of dwarf eelgrass are here the classic intertidal seagrasses (Green and Short, 2003), although most work on the ecology of their benthic macrofauna has been carried out not in estuaries but in shallow, semi-enclosed, but relatively high-salinity

coastal habitats (e.g. Wolff et al., 1993; Lee et al., 2001; Blanchet et al., 2004; Skilleter et al., 2006; Berkenbusch et al., 2007; Pillay et al., 2010). This includes the earlier studies of their spatial ecology that have been sited in Moreton Bay (Queensland, Australia), in the southern North Sea (UK) and in the marine embayment into which the South African Knysna estuary discharges (Barnes and Hendy, 2015; Barnes and Hamylton, 2015). A remarkable degree of spatial uniformity has been found at these sites in both functional diversity and functional composition across small (<0.4 ha) to medium distance scales (2-6 km), as well as from locality to locality; the Australian and South African systems being particularly similar. Nevertheless, Barnes and Hendy (2015) were also able to analyse some preliminary data from along the Knysna estuarine gradient, and although no significant differences between the frequencies of the various functional groups could be detected, it did appear that there were decreases in functional diversity and in the number of functional groups along its long axis.

Many gaps in our understanding of how such seagrass-associated assemblages function under estuarine conditions remain, and these include the effects of environmental gradients in modifying their structure. For example, do changes in functional diversity mirror those in species diversity, and do different functional 'groups' (Hooper et al., 2002) or 'guilds' (Franco et al., 2008) penetrate estuarine seagrass beds to different extents, thereby altering local functional structure, and, if so, why? Previous work in this field has subdivided estuarine invertebrate assemblages into only a

very limited number (4-7) of very broad trophic categories, e.g. 'sub-surface detritus feeders', 'carnivores', 'omnivores' and 'filter feeders' (Gaston et al., 1998; Gilberto et al., 2004; Gaudêncio and Cabral, 2007; Conde et al., 2013). Whilst being aware of the difficulties of attribution of generalist feeders to specific trophic categories (Macneil et al., 1997), here we attempt a more intensive functional analysis, incorporating elements of size, life-style, mobility and anatomy as well as of trophic group. Using such a system, the purpose of the present study was to examine the spatial distribution of the component functional groups of the seagrass-associated macrofauna in considerably more detail in order to test the null hypothesis that there are indeed no significant differences between the frequencies of the various functional groups along a main estuarine channel, and to compare earlier data on the linear spatial patterns of biodiversity generated by species assemblages (Barnes and Ellwood, 2012) with those of their functional groups.

## **2. Materials and methods**

### *2.1 Study sites*

Macrofaunal sampling was conducted over 11 weeks in the 2015 austral summer at six localities in the Knysna estuarine system, Western Cape, RSA (an 'estuarine bay' in the terminology of Whitfield, 1992), a system described in detail by Russell et al. (2009). Knysna supports the largest area of seagrass (some 350 ha) and highest macrofaunal biodiversity

of any South African estuary (Turpie et al., 2002; Bandeira and Gell, 2003), with >100 macrobenthic species in its *Zosterella capensis* beds (Barnes and Ellwood, 2012), although almost 10% of these are on Mead et al's (2011) and other lists of introduced aliens. As seen in other estuaries (e.g. Ysebaert et al., 1998; Sousa et al., 2008), similarity profiling of earlier Bray-Curtis data from Knysna (Barnes, 2013a) identified a number (here 5) of significantly different variants of the estuary's intertidal fauna along the long axis of that system, corresponding to those in exposed clean sand near the mouth, and in the muddier sediments of the marine outer basin, the lagoonal-like central region, and the lower and upper sections of the estuary proper (see Largier et al., 2000; Allanson et al., 2000). The six localities of the present study (Fig. 1) were selected to represent each of these five variants of the system's macrofaunal seagrass assemblage together with the sharp ecotonal zone between the upstream and downstream regions demonstrated by Barnes & Ellwood (2012) (Fig. 2). Near the mouth, seagrass occurred only as a series of large patches across the extensive, relatively clean sandflats on the eastern shores of the main channel. Locality '1' was sited in this high-wave-action zone of the marine outer basin (34°04'03"S, 23°03'19"E), 1.5 km upstream. Over the remaining part of the estuary from some 2 km from its mouth to >15.5 km upstream, the entire shore below the level of the upper-shore saltmarsh was clothed in a virtually continuous belt of seagrass; i.e. from some 20 cm below MHWN level (decreasing upstream to ≈50 cm below) down to the sublittoral zone (Maree, 2000), the mean tidal range being ≈1 m. The five upstream localities were sited in this belt:

'2' (34°03'31"S,23°02'02"E) - still within the marine outer basin but 4 km upstream;

'3' (34°02'31"S,23°00'59"E) - 8 km upstream, in the lagoonal zone;

'4' (34°03'00"S,22°59'58"E) - 10 km upstream, in the upstream/downstream boundary region;

'5' (34°02'00"S,22°59'42"E) - 12 km upstream, in the lower estuary; and

'6' (34°00'58"S,23°00'10"E) - 15 km upstream, in the upper estuary.

## 2.2 Protocol

Four replicate sites were established at each locality at intervals of >75 m, with each site at localities 2-6 being sampled by 10 replicate core samples 1 m apart in a line parallel to the water's edge between MLW and LWS levels. Samples from locality 1 sites were taken from within four different patches. As previously at Knysna (Barnes, 2013b; Barnes & Barnes, 2014), individual cores were of 55 cm<sup>2</sup> area and 10 cm depth, thus collecting the smaller species that overwhelmingly dominate most estuarine and other soft sediments and constitute the large majority of their invertebrate biodiversity (Gaudêncio & Cabral, 2007; Albano et al., 2011), though not the scarcer megafauna (e.g. *Bursatella*) or the deeply-burrowing species (e.g. *Marphysa*). All core samples were collected soon after tidal ebb from the area of shore concerned, and were gently sieved on site through 710 µm mesh. Retained material from each core was then: (i) placed in a large polythene bag of seawater within which all seagrass was shaken vigorously to dislodge all but sessile animals and was then discarded; (ii) re-sieved and transported immediately to a local laboratory, and (iii) there



placed in a 30 x 25 cm white tray in which the living fauna was located by visual inspection, this continuing until no further animal could be seen during a 3-minute period. Faunal individuals were separated into the component species and were counted. All species were assigned to one of 27 functional groups (FGs) (Table 1), based on those recognised in *Zosterella* beds by Barnes and Hendy (2015). Nomenclature below is as given by the World Register of Marine Species (WoRMS, [www.marinespecies.org](http://www.marinespecies.org), accessed April 2015) except for the unlisted "*Assiminea*" *capensis* (Sowerby) (see Miranda et al., 2014). Sessile and mobile species can differentially influence spatial patterns of biodiversity (Davidson et al., 2004), and this study excluded any sessile or semi-sessile animals (e.g. *Halcampaster*) that had become detached from the seagrass leaves during sampling. For comparative purposes, some additional material on a sixth variant of the system's seagrass macrofaunal assemblage that occurs in the marine basin in highly sheltered conditions well away from the main channel was obtained from the data underlying Barnes and Barnes (2014), i.e. from their 'Rex' and 'Armstrong' sites.

### 2.3 Data analysis

Overall diversity of each FG distribution was estimated by Hill's  $N_1$ , considered by Schleuter et al. (2010), etc. to be appropriate in the ecological and analytical circumstances, relative functional evenness by Pielou's  $J$ , as recommended by Jost (2010), and numbers of species and FGs as Hill's  $N_0$  (as 'densities' *sensu* Gotelli & Colwell, 2001). Variation in these metrics across localities was tested by one-way ANOVA and post hoc Tukey HSD

tests on the four component sites within each locality; and potential covariance of the relative importance of individual FGs was investigated via Pearson correlation-matrix analysis. Where necessary, proportional data were logit transformed before statistical analysis (Warton and Hui, 2011), with zero values being represented by the nominal proportion of 0.25 ind site<sup>-1</sup>. FG structure at the various sites was compared using the non-parametric multivariate techniques contained in PRIMER 6.1 [PrimerE Ltd: Plymouth Routines in Multivariate Ecological Research, Version 6.1]. Ordination by principal components analysis (PCO) with hierarchical clustering analysis using S17 Bray-Curtis similarity matrices were used to explore similarities between locality FG proportions. Similarity percentage analysis (SIMPER) was employed to examine site-specific FG structure. Similarities of FG occurrences between localities were examined using PERMANOVA. Variation in the proportion of the total comprised by the various FGs across localities was assessed by cross-tabulation followed by  $\chi^2$  tests of homogeneity (although 78% of the expected frequencies were  $\leq 5\%$ , and hence the test can be regarded only as approximate), and by one-way ANOVA of logit-transformed data. Relative importance of the various FGs, including for the construction of Whittaker diagrams, was assessed using indices of numerical importance, as earlier in respect of species data (Barnes, 2014).

### **3. Results**

The proportions of the total comprised by the various FGs were not uniform up the estuary ( $\chi^2 = 769$ , df 130;  $P < 0.001$ ). Whether using raw or logit-transformed proportions, PCO (Fig. 3) clearly demonstrates that the proportional FG structures of the six localities cluster into three significantly different blocks (PERMANOVA Pseudo- $F_{2,29} = 25.9$ ,  $P < 0.001$ ): (i) the sandy mouth region (locality 1) mainly characterised by FGs 18, 17, 6 and 7 (cumulative SIMPER 62%), (ii) the main body of the system (localities 2-5) characterised by FGs 4, 19, 22 and 6 (cumulative SIMPER 75%), and (iii) the upper estuary (locality 6) and the two sheltered but fully marine sites away from the main channel (Rex and Armstrong) characterised by FGs 17 and 22 (cumulative SIMPER 91%). Within the main marine/lagoonal/lower-estuarine block, three sub-regions of sites are also distinguishable at a Bray-Curtis similarity of 60% (PERMANOVA Pseudo- $F = 10.5$ ;  $P < 0.001$ ), but this segregation does not follow the longitudinal gradient. Locality 4, mainly characterised by FGs 24 and 4 (cumulative SIMPER 64%), was the only one to form its own separate cluster. The second block comprised three of the locality 2 sites, mainly characterised by FGs 4, 3, 13 (cumulative SIMPER 62%), and the third included localities 3 and 5 plus the remaining locality 2 site, mainly characterised by FGs 4, 19 and 22 (cumulative SIMPER 80%).

There were no significant differences (one-way ANOVA of logit-transformed proportions;  $F_{3,12} < 2.9$ ;  $P > 0.05$ ) between the proportions of 10 of the FGs across the component localities of this marine/lagoonal/lower-estuarine region (FGs 1, 2, 5, 8, 9, 13-15, 18, 25) but there were significant

differences in those of the remaining 14 present (FGs 3, 4, 6, 7, 10-12, 17, 19-24) ( $F_{3,12} > 4$ ;  $P < 0.05$ ) although post-hoc Tukey HSD tests showed no significant differences between any individual localities in respect of three of them (FGs 4, 19 and 22). In only two cases, however, was there a significant correlation between the proportions of any of these FGs and the estuarine long axis, those of FG 6 being negatively correlated ( $R = -0.75$ ;  $P < 0.0001$ ) and of FG 22 positively so ( $R = 0.78$ ;  $P < 0.0001$ ). Equivalently, the abundance per unit area of FG 6 also significantly decreased upstream ( $R = -0.76$ ;  $P < 0.0001$ ) whilst that of FG 22 increased ( $R = 0.53$ ;  $P < 0.009$ ). Most of the significant differences in proportions that did occur concerned locality 2 *vs* 4 and 5, but at least two FGs differed in their proportions at each of the other four potential locality pairings. Of the 12 FGs that together accounted for 85% of the total numerical importance, only four did not extend throughout the main channel: FG 18 was only present at the sandy mouth, FGs 13 and 24 only occurred across the central localities 2-5, and FG 6 (the subsurface-material ingesting scolecidan worms) was the only one to occur throughout the five seaward localities but fail to penetrate the low-salinity upper estuary. Apportioning the various FGs to one of six broad categories — (a) subsurface predators, (b) surface predators, (c) subsurface deposit feeders, (d) interface deposit feeders, (e) suspension feeders and (f) surface biofilm grazers — showed no differences between any of the localities in the logit-transformed proportions of (a), (c), (d) or (e), and of surface predators (b) only with respect of locality 4. For only the biofilm-grazers (f) were there marked differences between localities (between all pairings except 2 *vs* 3) (ANOVA  $F = 42$ ;  $P < 0.0001$ ).

The variable rank orders of the more important FGs at each locality are displayed in Table 2 (Kendall Coefficient of Concordance = 0.05;  $P > 0.9$ ). Excluding the poorly-represented individual FGs (those with <10 individuals in total) and those restricted to the system's sandy mouth, their distributions fell into five general categories (Fig. 4): (i) those present in numbers throughout the system (e.g. FGs 1, 9, 11 and 12); (ii) those decreasing in proportional importance upstream (e.g. FGs 6, 7, 10 and 14); (iii) those increasing in proportional importance upstream (e.g. FG 22); (iv) those most important over the central body of the system (e.g. FGs 4, 13, 19 and, in extreme form, 24); and (v) and those most important at the two extreme ends (e.g. FG 17). The only significant correlations (all negative;  $P < 0.005$ ) between proportional representation of the most important FGs were between nos 4 and 17, 4 and 19, 6 and 22, and 12 and 24. Individual FGs were not necessarily composed of the same faunal elements all along the gradient, however. Most noticeably, FG 17 (the biofilm-grazing microgastropods) was represented by the cerithioid *Alaba pinnae* at locality 1 (and less commonly at localities 2-5) but by the truncatelloids *Hydrobia knysnaensis* and "*Assiminea*" *capensis* at locality 6; whilst in FG 4 (interface-feeding canalpalpatan worms), *Caulleriella* was centred on localities 2-3, *Cirriiformia* on 3-4 and *Prionospio* although occurring throughout and in numbers at 2-4 was the dominant form at locality 5. No FG at the upper-estuarine locality contained more than two species, and four FGs (1, 4, 9 and 10) showed a significant decrease in the number of component species along the estuary ( $R > -0.86$ ;  $P < 0.03$ ).

Despite this considerable variation in the specific identity of the more important FGs at each locality, the highest-ranked eight FGs at each main-channel locality all fell on the same Whittaker-plot line (Fig. 5). Thereafter, however, the slopes of the less important ones became separated in sequence along the estuarine gradient as a consequence of their relative numbers (Fig. 5). The distribution of various FG metrics per site along the long axis of the system is shown in Fig. 6, as, where relevant, are the corresponding metrics based on the distributions of the component species.  $N_1$  species diversity,  $N_1$  FG diversity,  $N_0$  species density and  $N_0$  FG density were all non-uniformly distributed along that axis, as was overall assemblage abundance (one-way ANOVA  $F_{5,18} > 11$ ;  $P < 0.0001$ ), whereas variation in functional evenness and in  $N_0$  density of the more important FGs (those individually containing  $\geq 5\%$  of the total numbers) did not depart from random ( $F_{5,18} < 2.6$ ;  $P > 0.05$ ). In respect of the significantly-different species metrics, post-hoc Tukey HSD tests showed that localities 1-3 and 4-6 formed blocks within each of which there were no significant differences but between which (i.e. between 1/2 and 4-6) there were ( $P < 0.02$ ). There were no significant differences, however, between the intermediate locality 3 and either 1/2 or 4-6. The magnitudes of all metrics were significantly negatively correlated with distance up the estuarine long axis (Pearson  $R > -0.60$ ;  $P < 0.002$ ). In terms of total values per locality, FG  $N_0$  and  $N_1$  both fell by  $< 50\%$  from localities 2 and 3 to the upper estuary, whereas species density fell by  $> 67\%$ .  $N_0$  for the major FGs, however, fell by only  $11\%$ . In respect of values of  $N_0$  for those FGs each supporting  $> 1\%$  of the total animals at each locality, although the correlation with distance upstream

approached significance for the zone from 4 km to 15 km ( $P = 0.051$ ), it was not significant through the lagoonal and estuarine region (8-15 km) ( $P > 0.3$ ), each locality supporting 9-11 such FGs.

#### **4. Discussion**

Change in either the number or nature of FGs can effect the functioning of the systems they comprise (Emmerson et al., 2001; Hooper et al., 2005; Cardinale et al., 2006). Transitional systems such as estuaries are dominated by both spatial and temporal environmental change (Basset et al., 2013), however, and hence habitat filtering (De Bello, 2012) will restrict components of animal assemblages to those highly resilient forms able to withstand all but the more severe perturbations (Elliott and Quintino, 2007; Elliott and Whitfield, 2011; Dolbeth et al., 2013). Further, seagrass faunas are characterised by relatively generalist species (Boström et al., 2006; Vafeiadou et al., 2013; Scipione, 2013) and hence their assemblages are particularly likely to be able to absorb compositional change with less impact than those dominated by specialists (Clavel et al., 2011). It could therefore be predicted that individual FGs should have wide ranges within an estuarine seagrass environment. Such indeed appears to be the case within the Knysna estuarine bay. Only three of the more important FGs present to seawards did not also occur in the upper estuary. Two of these were very local in distribution, occurring at only a single point (although there in abundance). The infaunal suspension-feeding gastropod

FG 18, solely comprising *Turritella capensis*, was restricted to clean sandy sediments at the mouth, and the seagrass leaf-biofilm consuming starfish of FG 24, solely comprising *Parvulastra exigua* (see Jackson et al., 2009), only occurs under sheltered 'lagoonal' conditions, such as at locality 4, where wave action cannot cause them to be dislodged from the leaves (see Schanz et al., 2002; Roediger and Bolton, 2008). *Parvulastra* also occurs in other sheltered situations at Knysna well away from the main channel (Barnes and Barnes, 2014), but as a component of the South African seagrass fauna, it is otherwise known only from Langebaan Lagoon (Branch & Branch, 1980). Presumably the very low salinities of the upper estuary would prevent them from colonising that zone (Stickle and Diehl, 1987) although the relatively poor development of the seagrass beds under the same salinity conditions are likely to have a similar effect. The only other missing FG, the scolecidan consumers of subsurface organics (FG 6), was not encountered by this survey but scolecidans were recorded from the upper estuary by the earlier survey of Barnes and Ellwood (2012), although their relative importance, and indeed abundance, were inversely correlated with distance upstream. In effect, all major FGs widely occurring from the marine zone to the lower estuary are therefore also known from the upper estuary.

Other data also indicate a general lack of relationship of FGs with distance upstream and suggest degrees of spatial constancy *per se*. The proportions of 40% of the FGs did not vary along the long axis, for example; the number of major FGs present at points along the estuary showed only



random variation, as did their functional evenness; and five of the six major categories into which the FGs could be placed showed no spatial variation. In contrast, however, all FG metrics were negatively correlated with distance upstream, although changes were less marked than those of species density and diversity. Further, spatial variation of some form was demonstrated by 60% of the various FGs present in the main section of the system (corresponding to normal low-tide salinities of 35 to 20), including all but two of the ten most important ones (although, except in two cases, not in relation to its long axis, and in one of those two the relationship was positive not negative); and the rank order of importance of the FGs at each locality was far from uniform. Levels of spatial functional variation are thus considerably greater than observed over similar distances in more fully marine coastal *Zosterella* beds (Barnes and Hendy, 2015), as might be expected along such a marked environmental gradient as that within an estuary, but they are less than would perhaps be suggested by the classic variation in species density.

Some eight to ten major FGs characterised the whole estuarine system, as well as those of the equivalent coastal marine *Zosterella* beds reviewed by Barnes and Hendy (2015). The most significant of these were, in descending order of numerical importance, (i) infaunal worms feeding at the sediment surface via ciliated tentacles, palps or equivalent structures, (ii) infaunal suspension-feeding bivalve molluscs, (iii) epifaunal biofilm-grazing microgastropods, and (iv) epifaunal scavenging nassariid gastropods. Proportional importance of the tentaculate worms was negatively correlated

with those of both the microgastropods and the nassariids, whilst the sharp peak in *Parvulastra* importance also coincided with a trough in that of the tentaculate worms as well as in that of the hymenosomatid crab that may prey on them (Melrose, 1975; Richer de Forges, 1977). Such polychaetes have been considered to require continual water movement to renew their food materials (Newell et al., 1984) and this may be prevented by the denser and longer seagrass leaf canopies that characterise sheltered areas and that are likely to support more leaf-associated grazers (Schanz et al., 2002), whilst movement across the sediment surface by numerous nassariids may disrupt their tentacular feeding systems (see Van Colen et al., 2013). Other characteristic major FGs were infaunal subsurface-feeding scolecidan and carnivorous errantian worms, epifaunal percaridan crustaceans, small epifaunal predatory crabs, and infaunal but surface microphytobenthos-feeding ocy podoid crabs. The proportional importance of the infaunal scoliceidans and bivalves were also negatively correlated, possibly consequent on interference (Kelaher et al., 2003). At Knysna, and elsewhere (e.g. Asmus and Asmus, 2000), the same FGs also dominate unvegetated soft sediments, the seagrass-leaf associated biofilm-grazing microgastropods then feeding on the sediment surface instead (Barnes and Barnes, 2014), possibly including on carbon emanating from the adjacent seagrass beds (Connolly et al., 2005).

Those results above that relate to the distribution of individual species along the main channel of the Knysna estuarine bay largely confirm the earlier ones of Barnes and Ellwood (2012). In particular, that the system is

divisible into two sections (here localities 1-3 and 4-6) within each of which there is a degree of uniformity in species biodiversity but between the members of which there are significant differences. The earlier study showed that number of species more than halved between the marine basin and upper estuary, and such was the present case too. This division of the system into two sections with respect to species distributions does not, however, correspond to any compartmentalisation apparent from functional ecological considerations. Decrease in species density along the gradient is then mainly a consequence of reducing numbers of species within individual FGs rather than decreasing numbers of major FGs, multi-species FGs each losing on average 0.8 species between the marine/lagoonal region and the lower estuary, and 1.5 species by the upper estuary. These are relatively low levels of redundancy, as appears typical for estuarine FGs (Magalhães and Barros, 2011; Dolbeth et al., 2013). Even in fully marine intertidal seagrass systems each FG tends to be dominated by a single species (Barnes and Hamylton, 2015). Guilds with the greatest within-FG diversity were the surface-feeding predatory worms, the interface-feeding canalpalpatans and the subsurface organics consuming scolecidans. Monitoring the diversity of FGs such as those may provide a means of detecting changes to system function.

A further major difference between species-assemblage and functional-group diversity divisions of the Knysna system concerns the upper estuary. In terms of their macrofauna, the upper and lower estuary formed a single cluster separate from those of the sheltered marine sites (Barnes, 2013a:

Fig. 2). In terms of F-G relationships, however, the upper estuary clustered with the sheltered marine sites whilst the lower estuary clustered, separately, with the lagoonal and one of the marine-basin ones. SIMPER showed that underlying the similarity between upper estuarine and sheltered marine sites was the shared dominance of the leaf-biofilm grazing microgastropod FG, and the unimportance of that group at localities 2-5. The species concerned were the truncatelloids *Hydrobia knysnaensis* and "*Assimineia*" *capensis*. In fact these two displayed the only marked change observable at localities sampled in both 2012 and 2015. At the time of the earlier survey, the truncatelloids attained densities of  $\approx 8,000 \text{ m}^{-2}$  in the upper estuary, whereas at the same time of year in 2015 although they were still the dominant faunal component their numbers were only some 10% of those found earlier. [Marked fluctuations in abundance seem typical of microgastropods at Knysna (Barnes and Barnes, 2014) and elsewhere under estuarine and lagoonal conditions (Barnes, 1991), although the causes remain elusive.] The pattern of relationships demonstrated in 2015 clearly occurred in spite of these density changes, rather than because of them, in that lesser importance of FG17 would be expected to result in greater similarity of the upper and lower estuary zones, not lower. One clear feature of this situation, however, is that the occurrence of *H. knysnaensis* and "*A.*" *capensis* along the main channel only in the upper estuary is not related to the longitudinal salinity gradient. Within the context of the whole estuarine system, the one environmental feature that does unite the low-salinity upper estuary and the sheltered marine zone away from the main channel, as well as distinguish both from the other sampled localities (with

the partial exception of locality 4) is shelter from wave action (see, e.g., Callaghan et al., 2015). It could be argued that at the relatively sheltered locality 4 *Parvulastra* replaces leaf-associated molluscs (although cf Branch and Branch, 1980). As above, the low salinity in the upper estuary probably prevents the occurrence there of this echinoderm, whilst it is abundant in the seagrass of the sheltered marine zone. The effect of wave action on seagrass-leaf associated microgastropods, and on seagrass biofilm grazers in general, would repay further study.

Studies of the relative body-size patterns of predators and their prey (Emmerson and Raffaelli, 2004) and of the complementary channels through which energy may flow (Lobry et al., 2008) have argued in favour of considerable stability and resilience in estuarine food-webs. This is also suggested here by the relatively conservative patterns of estuarine functional structure and diversity along the upstream gradient/s, notwithstanding the characteristic diminution in species density and diversity.

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**Table 1.** Macrofaunal functional groups occurring in the Knysna seagrass beds (after Barnes and Hendy, 2015) to which the individual species were allocated.

<u>Group No.</u>	<u>Diagnosis of group</u>
1	Subsurface-feeding, errant predatory worms (some nemertines & some errantian polychaetes e.g. nephtyids & glycerids); 4 spp
2	Surface-feeding, errant predatory worms (e.g. polyclads, many nemertines & errantian polychaetes); 9 spp
3	Surface-feeding, tubicolous or burrow-dwelling, omnivorous worms (e.g. errantian polychaetes such as many nereids); 4 spp
4	Deposit-feeding, tubicolous or burrow-dwelling worms with ciliated feeding palps, tentacles, etc., that collect material from the sediment surface (e.g. most canalpalpatan polychaetes); 12 spp
5	Suspension-feeding, infaunal, tubicolous worms (1 sp - the sabellid polychaete <i>Branchiomma</i> )
6	Subsurface, free-living or burrow-dwelling, microbe-, protist- or sediment-ingesting worms (e.g. most scolecidan polychaetes & tubificine oligochaetes); 8 spp
7	Mobile, suspension-feeding ostracod crustaceans (1 sp - <i>Cylindroleberis</i> )
8	Sedentary and often tubicolous, suspension-feeding peracaridan crustaceans (e.g. several corophiideans); 3 spp

- 9 Omnivorous, errant peracaridan crustaceans (e.g. sphaeromatoids); 6 spp
- 10 Algivorous, errant or occasionally 'nest'-inhabiting peracaridan crustaceans (e.g. an amphithoeid & idoteid); 2 spp
- 11 Predatory, errant peracaridan crustaceans (e.g. *Cyathura* and *Paramoera*), consuming small (often meiofaunal) prey; 3 spp
- 12 Large, errant, predatory decapod crustaceans (e.g. *Hymenosoma*) taking macrofaunal prey; 3 spp
- 13 Microphytobenthically-feeding, burrow-dwelling decapod crustaceans (camptandriids and the hexapodid *Spiroplax*); 3 spp
- 14 Omnivorous, errant decapod crustaceans (1 sp - *Diogenes*)
- 15 Suspension-feeding, burrow-dwelling decapod crustaceans (1 sp - *Upogebia*)
- 16 Relatively large periphyton and leaf-surface grazing gastropod molluscs (1 sp - *Gibbula*)
- 17 Epifaunal, epiphyllic bacterial and algal biofilm grazing microgastropod molluscs (e.g. truncatelloids & the litiopid *Alaba*); 4 spp
- 18 Sedentary, infaunal, suspension-feeding gastropod molluscs (1 sp - *Turritella*)
- 19 Predatory/scavenging, errant molluscs (e.g. neogastropods, nudibranchs); 3 spp
- 20 Ectoparasitic gastropod molluscs (pyramidelloids); 4 spp
- 21 Algivorous, errant gastropod molluscs (a saccoglossan & haminoeoid); 2 spp

- 22 Sedentary, infaunal, burrow-dwelling or buried, suspension-feeding bivalves (most bivalve molluscs); 11 spp
- 23 Sedentary animals dependent in whole or in part on chemosynthetic symbionts (lucinid bivalve molluscs); 2 spp
- 24 Epifaunal, epiphyllic bacterial and algal biofilm consuming asteroids (1 sp - *Parvulastra*)
- 25 Burrowing, deposit-feeding holothurians (1 sp - *Leptosynapta*)
- 26 Suspension-feeding errant ophiuroids (1 sp - *Amphipholis*)
- 27 Algal-grazing errant echinoids (1 sp - *Parechinus*)

**Table 2.** Rank orders of the eight numerically most important functional groups at each of the six localities, together with those in sheltered regions away from the main channel (S).

<u>Rank</u>	<u>Localities</u>						S
	1	2	3	4	5	6	
1 <sup>st</sup>	18	4	4	24	4	17	17
2 <sup>nd</sup>	17	3	19	4	19	22	9
3 <sup>rd</sup>	7	6	22	22	22	3	13
4 <sup>th</sup>	6	13	17	19	1	12	24
5 <sup>th</sup>	14	17	6	6	9	1	4
6 <sup>th</sup>	10	9	13	13	12	11	3
7 <sup>th</sup>	4	19	9	1	11	19	19
8 <sup>th</sup>	1	12	12	17	3	4	10



## Legends for Figs

1. Sampling localities in the Knysna estuarine system.
2. Position of sampling localities in relation to a representative low-tide salinity gradient along the long axis of the system (from Barnes and Ellwood, 2012) and to the ranges of the five variants of its macrofaunal seagrass assemblage (Barnes, 2013a).
3. Principal components analysis of the proportions of the total numbers in each functional group present at each of six localities along the long axis of the Knysna estuarine bay, with a detail of that of the main marine/lagoonal/lower-estuarine cluster.
4. Various patterns of distribution of functional groups along the main channel of the Knysna estuarine system (mean percentage of the total individuals per locality  $\pm$  SE).
5. Ranked functional-group importance curves for the six localities along the main channel of the Knysna estuarine system, importance being measured as percentage of total Index of Numerical Importance.
6. Distribution of assemblage metrics along the main channel of the Knysna estuarine system (mean values per site at each locality  $\pm$  SE):  $N_1$  species diversity and  $N_1$  functional group diversity;  $N_0$  species density,  $N_0$  functional-group density, and  $N_0$  major functional-group density; functional-group evenness; and overall abundance (numbers  $0.1 \text{ m}^{-2}$ ).

Fig. 1

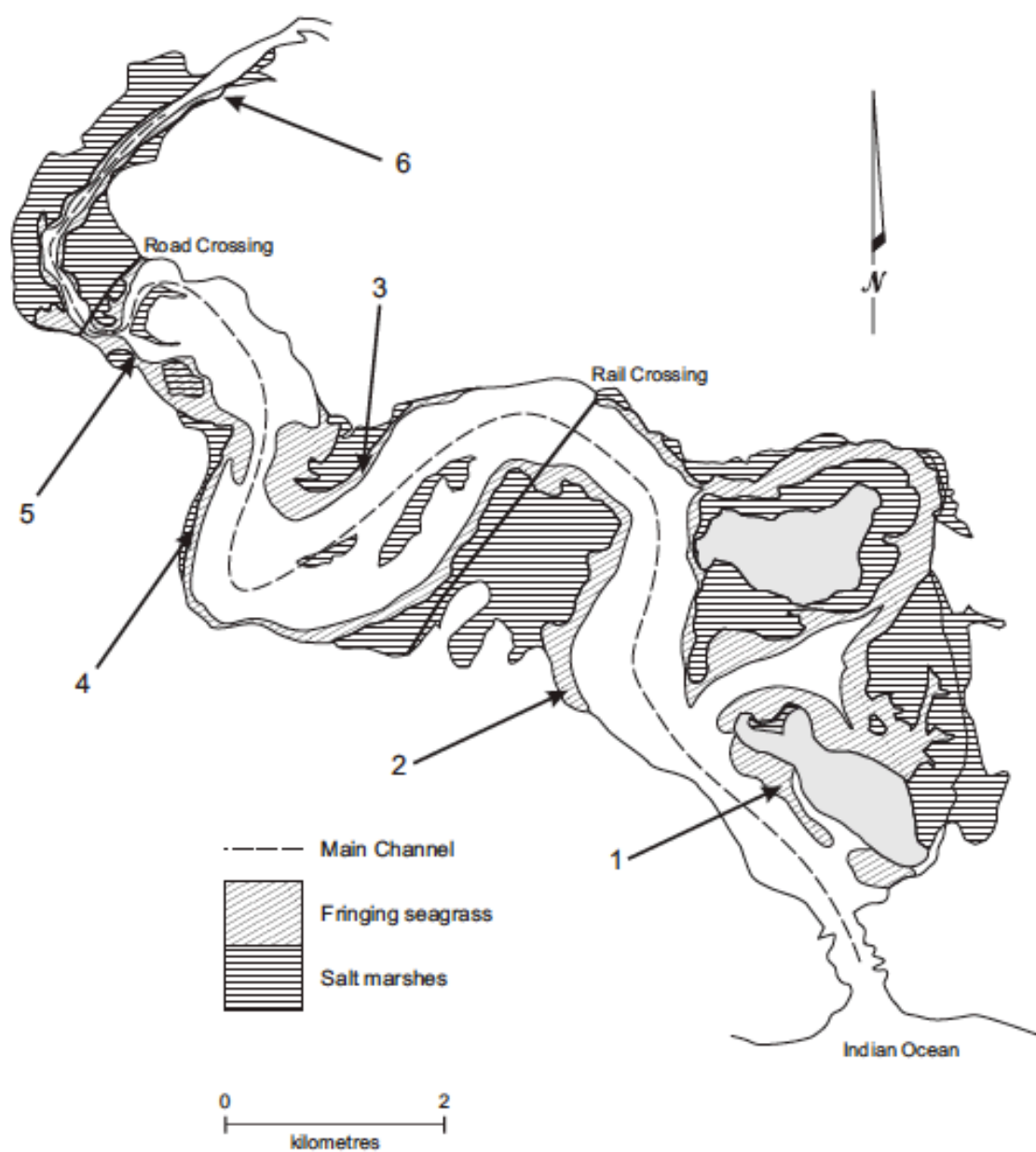


Fig. 2

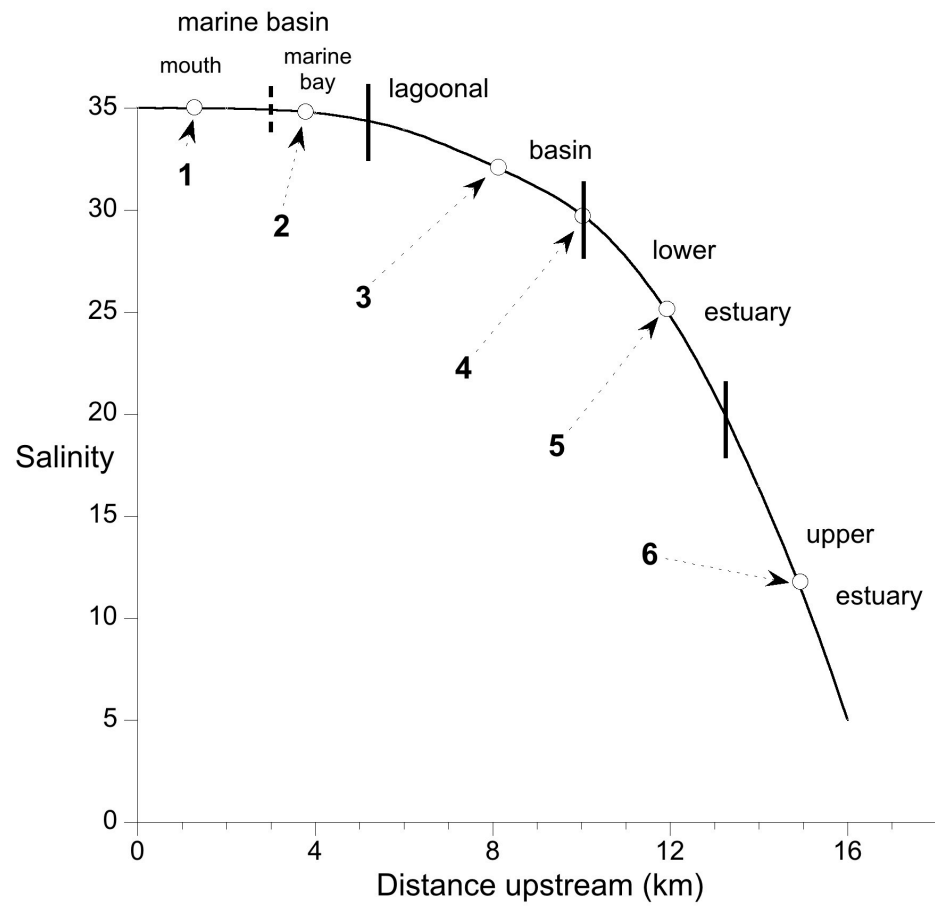


Fig. 3

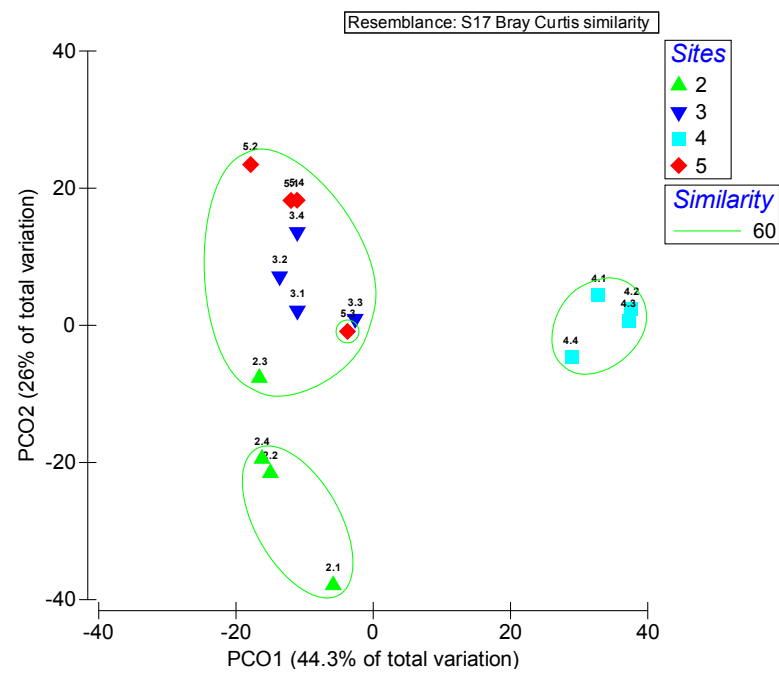
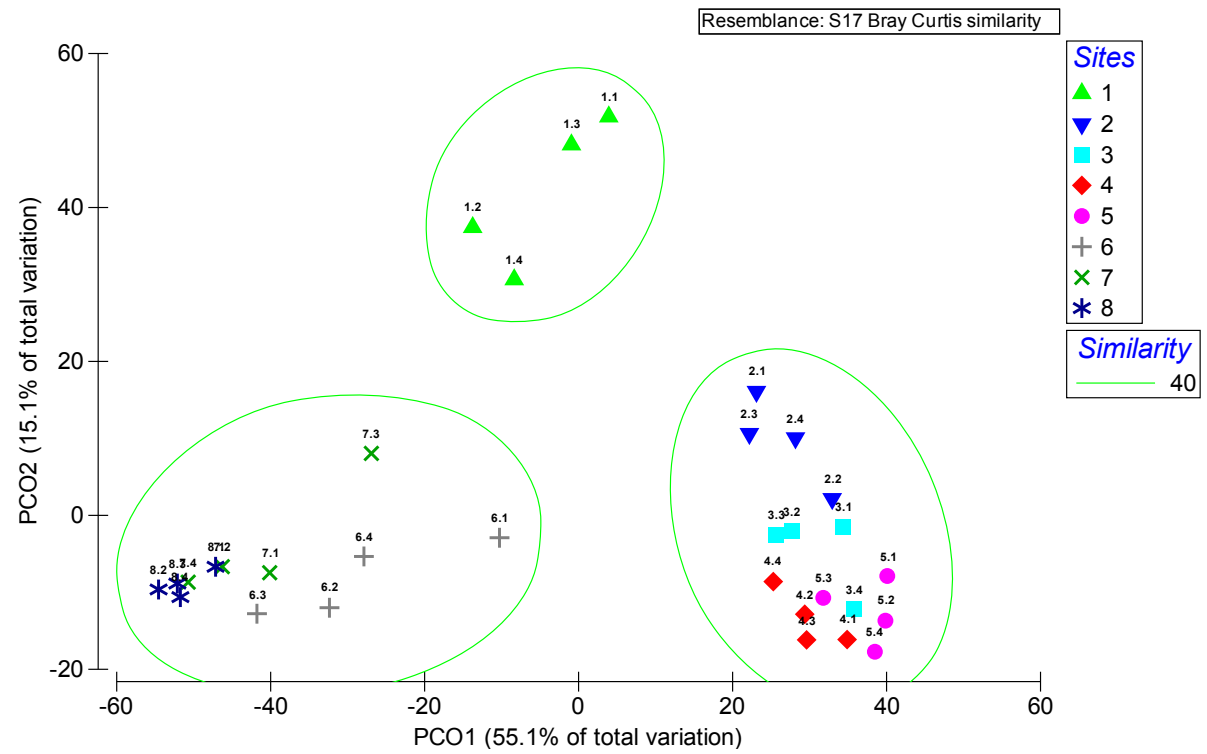


Fig. 4

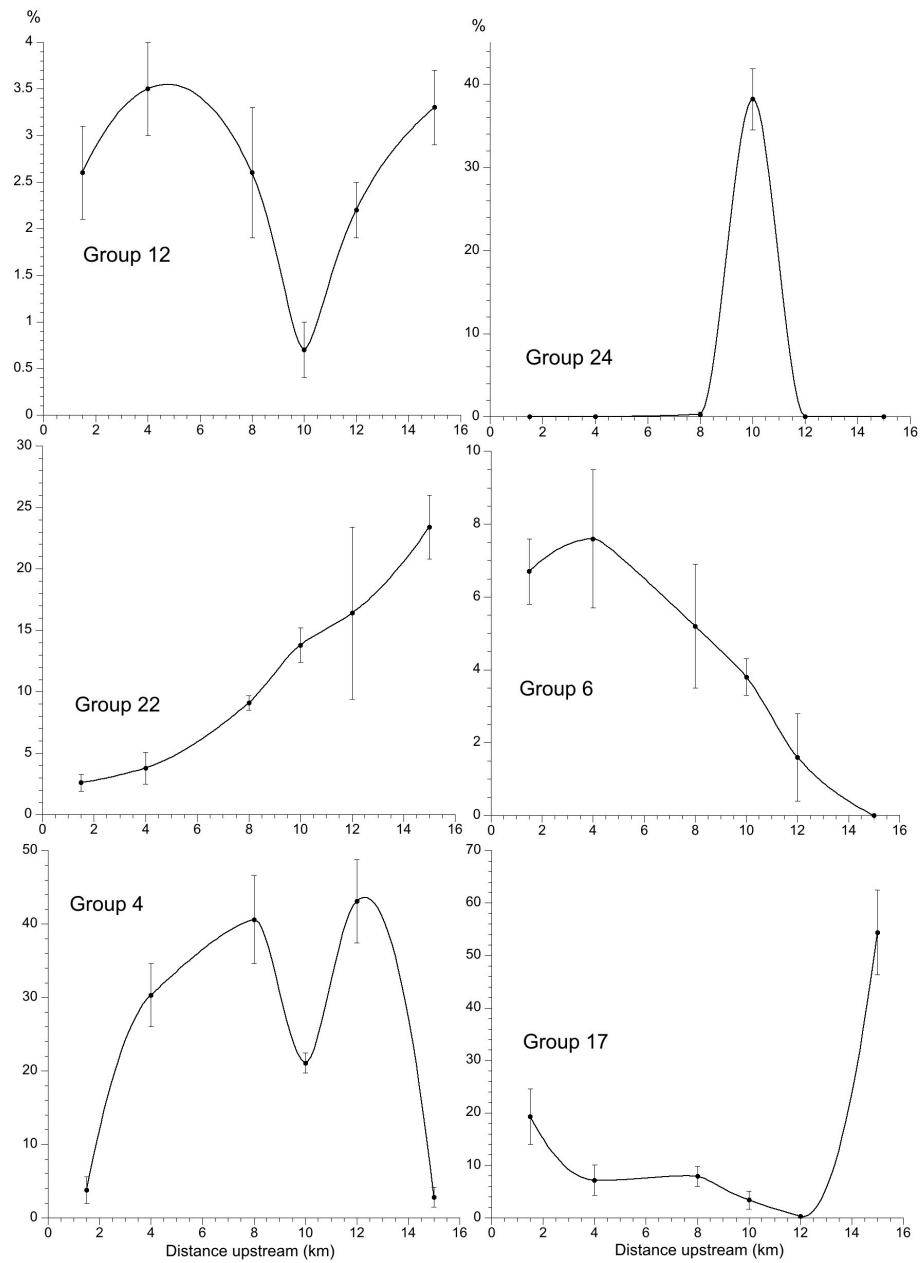


Fig. 5

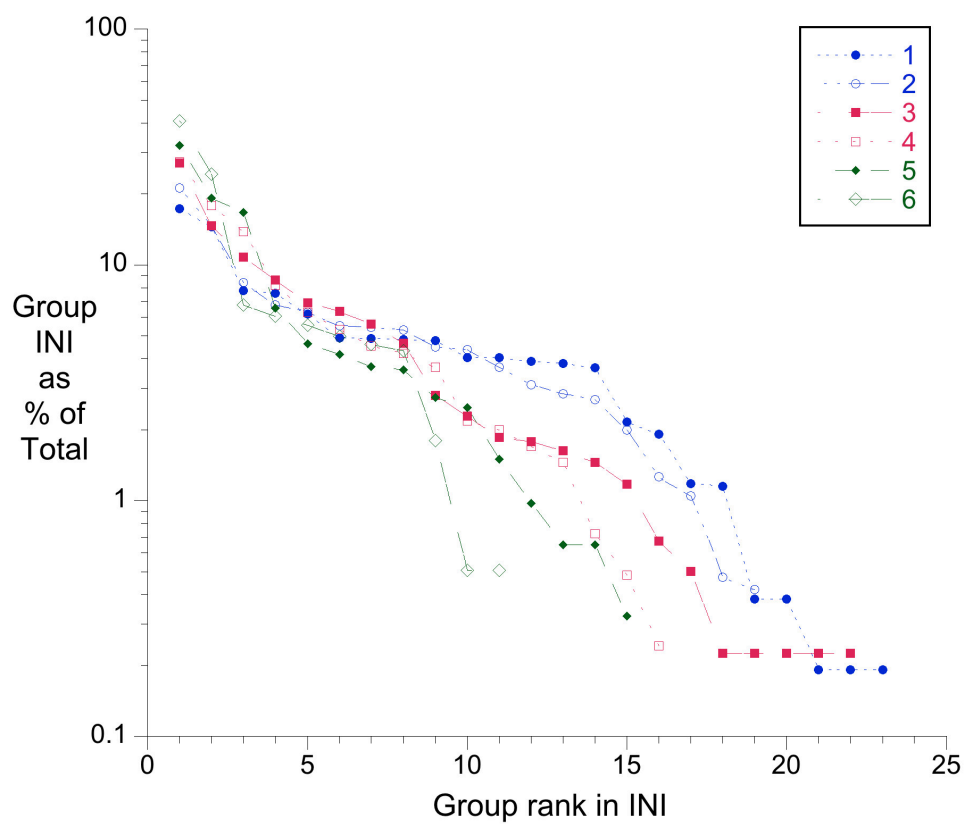


Fig. 6

